Community robustness and limiting similarity in periodic environments

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Abstract

Temporal environmental variation has long been considered as one of the potential factors that could promote species coexistence. A question of particular interest is how the ecology of fluctuating environments relates to that of equilibrium systems. Equilibrium theory says that the more similar two species are in their modes of regulation, the less robust their coexistence will be; that is, the volume of external parameters for which all populations persist shrinks with increasing similarity. In this study we will attempt to generalize these results to temporally varying situations, and establish the precise mathematical relationship between the two. Our treatment considers unstructured populations in continuous time with periodic attractors of fixed period length, where the periodic behavior is due to external forcing as opposed to being indigenously generated. Within these conditions our treatment is general. We provide a coherent theoretical framework for defining measures of species similarity and niche. Our main conclusion is that all factors that function to regulate population growth may be considered as separate regulating factors for each moment of time. In particular, a single resource becomes a resource continuum, along which species may segregate in the same manner as along classical resource continua. Therefore, we provide a mathematical underpinning for considering fluctuation-mediated coexistence as temporal niche segregation.

Keywords: regulation, niche, coexistence, fluctuations, structural stability, robustness

1 Introduction

Much of the early theory on coexistence concerned equilibrium situations (Volterra 1926, Gause 1934, Hardin 1960); the main conclusion was that if two or more species consume the same resources, only one will persist. Later Levin (1970) and Levins (1974) realized that this inference generalizes from resources to all those factors that are involved in a density-dependent feedback loop. After Krebs (2001, p. 288), Case (2000, p. 146), and Meszéna et al (2006) we will call these factors regulating variables (they are equivalent to what Levin 1970 and Chesson 1994 call limiting factors, and what Chesson and Huntly 1997 call competitive factors). The competitive exclusion principle then states that at equilibrium the number of coexisting species cannot exceed the number

of regulating factors. This simple picture emerging from equilibrium theory came under attack, however, from at least two quarters. First, the practical utility of the principle came into doubt. Second, the question arose whether fluctuating dynamics would invalidate the competitive exclusion principle, something that seems to depend on the equilibrium assumption crucially.

The problem of practical usefulness arises when there are infinitely many regulating factors and therefore there is no upper limit to the number of coexisting species. Though MacArthur and Levins (1967) argued persuasively that limiting similarity is the expected behaviour in the context of the Lotka–Volterra model, the work of May and MacArthur (1972), May (1973) and Roughgarden (1979) demonstrated that it is always possible to have arbitrarily tight species packing, suggesting that the competitive exclusion principle is more of a mathematical curiosity than an empirically relevant idea (Rosenzweig 1995). On the other hand, it has been observed mathematically that while there is no fixed lower bound to similarity, not all configurations are equally robust: certain coalitions of species are more sensitive to external perturbations than others. While coexistence of similars is possible, it is restricted to a narrow range of environmental parameters. Therefore, the limiting similarity principle can be recovered by shifting the emphasis from analyzing the *stability* of coexistence to looking at its *likelihood*, i.e. how wide or narrow is the range of parameters that allow for the persistence of all populations within the system ("coexistence bandwidth", Armstrong and McGehee 1976). Large volumes of parameter space allowing for coexistence are called robust systems; narrow ranges are called unrobust. A system with a very narrow coexistence bandwidth, i.e. one that is unrobust is unlikely to persist for long, and therefore some sort of limits to similarity are expected to emerge after all. This new, reformulated limiting similarity principle will only be useful though if robustness decreases with increasing similarity, independent of model details, at least for species that are already similar enough. That this is so has been demonstrated rigorously for fixed point models by Meszéna et al (2006). They showed that as species get more similar in how they relate to the regulating factors (more specifically: if species growth rates show similar sensitivity to a change in the regulating variables, or the species have similar impacts on the regulating factors) then the robustness of their coexistence declines to zero. Hence the criticism of the competitive exclusion principle that it is unable to address the question of how similar two species may become has been resolved through considering the robustness, as opposed to the stability, of coexistence.

However, there remains the second important criticism of the competitive exclusion principle, namely that the ubiquity of temporal fluctuations in real ecosystems calls the equilibrium assumptions behind the principle (and behind the more modern theory of robustness of coexistence) into question. The consequences of the equilibrium conditions were thought to lose validity in a fluctuating system (Hutchinson 1961). Presumed invalidity of the competitive exclusion principle was developed into an ecological world view by Huston (1979). However, as Abrams (1983) and Chesson (1991) pointed out, the need for ecological segregation is not alleviated by environmental fluctuations: it just seems to be that way if we look at segregation strictly in the sense of resource partitioning. Chesson and Huntly (1997) not only argued for the verity of the need for ecological segregation but demonstrated the flaws inherent in those theories that look upon fluctuations as a means to invalidate the competitive exclusion principle.

Rigorous theories of coexistence in a fluctuating environment also imply the need for ecological segregation. Levins (1979) established the role of higher moments as effective regulating factors in situations where the densities are fluctuating arbitrarily in a bounded region of phase space. This means that e.g. the time-average and variance of a resource both act like effective resources and thus two species could stably coexist on them – provided that interspecific competition between the two species "consuming" the mean and the variance of the resource is lower than intraspecific competition within each of the species. Chesson (1994, 2000, 2009) provided a classification scheme for the coexistence maintaining mechanisms. Beyond fluctuation-independent niche segregation, he established the "effect of relative nonlinearity" (which occurs when species have different nonlinear responses to competition) and the "storage effect", which is based on species-specific responses to the environment, covariance between the environment and competition, and buffered population growth. His approach is based on a small-fluctuation approximation. Intuitively, the storage effect is considered a mathematical representation of temporal niche segregation (Chesson and Huntly 1997, Chesson 2000).

In this paper we aim to provide a solid ground for the concept of temporal niche segregation and its role in maintaining coexistence. That is, we intend to formalize the commonality between temporal and more conventional types of niche segregation. Our starting point is Meszéna et al (2006), that has already provided that commonality in a stable environment. We restrict our attention to externally forced periodic dynamics with a fixed period T. Moreover, we assume the dynamics of the regulating variables to be fast compared to population dynamics. Within these restrictions we keep our considerations general. In particular, we do not need the assumption of small fluctuations. In Meszéna et al (2006) the common ground was segregation with respect to the regulating variables. In line with this biological intuition, here we consider the regulating variables at different instants of time to be different regulating variables. In this scheme temporal niche segregation is also a type of differentiation with respect to regulating variables. Therefore, all considerations in Meszéna et al (2006), especially decreasing robustness with increasing similarity, carry over to the fluctuating case. We will discuss the realationship between our and Chesson's (1994) formalization as well.

We begin by introducing the fundamental concept of regulating factors (Section 2), and then reviewing the basic framework for fixed points in Section 3. Then, in Section 4 we extend the theory to periodic orbits in phase space and rederive the basic formulas in a periodically fluctuating environment. Finally, as a demonstration we apply the results to a simple example in Section 5.

2 Regulating factors

Populations with fixed demographic parameters grow exponentially – but, since the parameters usually dependent on density and external influences, population growth can take on virtually any form. However, one may still treat any change in population densities as locally exponential in time, where the instantaneous growth rate is a function of both density dependent and independent variables. Taking density dependence into account, one can introduce the concept of regulating factors: the set of variables involved in the feedback between growth rates and densities. In other

words, *all* interactions between the individuals of the populations have to be mediated by the regulating variables: fixed values of these factors would lead to the exponential growth of all species in the community.

In this context, the growth of any population in any model may be written as

$$\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} = r_i\left(\mathbf{R}(x_1(t),\ldots,x_L(t)),E,t\right) \qquad (i=1,\ldots,L), \tag{1}$$

where $x_i(t) = \ln(n_i(t))$ is the natural logarithm of the ith population's density $n_i(t)$ at time t (the logarithmic scale having been introduced for future convenience), r_i is the growth rate of the ith population, E is the collection of environmental and all other density-independent parameters (the "external" variables), L is the total number of species in the system and $\mathbf{R}$ is the vector of regulating factors (the same as $\mathbf{I}$ in Meszéna et al 2006), which of course is a function of the densities. In case one has environmental parameters that fluctuate with time, only the time-independent parts go into E and the rest should be considered as an explicit time dependence of the growth rates. For example, if a certain ecological situation causes the (density-independent) intrinsic rate of growth r_0 to fluctuate as $r_0 = a(1+\varepsilon\cos(\omega t))$, then the vector E refers to the parameters a, ε and ω, not r_0 as a whole. One does not lose generality by this choice of convention, and it will make differentiation of r_i with respect to E more convenient later on.

There are two things neglected by Eq. (1). First, it considers unstructured populations only. Second, it assumes that $\mathbf{R}$ depends on the instantaneous values of the population densities – in other words, it disregards time lags in the regulation of populations. Apart from these restrictions however, these population dynamical equations are general: any continuous time, continuous density model may be stated in the form of Eq. (1).

The vector of regulating factors $\mathbf{R}$ deserves special attention. In general, its elements will include resources, predators, and other discrete entities. But the number of regulating factors is not necessarily finite. The paradigmal example for infinite dimensional regulation is the resource continuum, e.g. the continuum of foods of different sizes. In this case, the function $q \mapsto R(q)$ constitutes the vector $\mathbf{R}$, where $R(q)$ denotes the concentration of food with size q. One can consider q as a continuous index of the vector $\mathbf{R}$. In general, the continuous index variable can be more than one dimensional (e.g. describing size and hardness of the food). It is also possible to have discrete and continuous indices at the same time, e.g. if two different kinds of food both have size-distributions, or if a food size continuum *and* various predators function to regulate the populations. To emphasize the role these indices play in our analysis, here we adopt the notational convention that the **boldface** type will be reserved for quantities that carry the same indices as $\mathbf{R}$.

3 Summary of the fixed point theory

3.1 Limiting similarity of species

The idea behind Meszéna et al's (2006) general theory of niche and limiting similarity is to realize that any system will behave like the Lotka–Volterra model near a stable fixed point. One therefore

has to linearize the growth rates around the equilibrium point and analyze the robustness (i.e. the range of parameters where all densities are positive) of the simpler linear model (May 1973, Vandermeer 1975). Dynamical stability of the community, i.e. negative real parts of the eigenvalues of the community matrix, is assumed (there is no point in looking at the robustness of a dynamically unstable system). To obtain the set of parameters that allows for coexistence, one calculates the response of the densities to a change in the external variables E. A wild response even to small changes indicates unrobust coexistence, one that is oversensitive to external perturbations and is therefore unlikely to persist for long.

So we have to take the set of equilibrium equations and differentiate them with respect to E. At a fixed point attractor Eq. (1) becomes time-independent so that the left hand side is zero, and the growth rates on the right hand side are independent of time. Since at a fixed point all growth rates are zero, we have L algebraic equations:

$$r_i\left(\mathbf{R}(x_1^*,\ldots,x_L^*),E\right)=0, \tag{2}$$

where the asterisk in the superscript refers to equilibrium values. Implicit differentiation with respect to E yields

$$\frac{\partial r_i}{\partial E}+\sum_{j=1}^{L}\frac{\partial r_i}{\partial \mathbf{R}}\frac{\partial \mathbf{R}}{\partial x_j}\frac{\mathrm{d}x_j^*}{\mathrm{d}E}=0, \tag{3}$$

where summation (integration) for all discrete (continuous) indices of $\mathbf{R}$ is understood in the scalar product $(\partial r_i/\partial \mathbf{R})(\partial \mathbf{R}/\partial x_j)$. This formula yields the linearized growth rates as a function of the perturbations of the densities, and as such, connects an arbitrary ecological model with the classic Lotka–Volterra equations.

The first factor of this scalar product describes the response of the ith growth rate to a change in the regulating variables, i.e. the sensitivity of the population to changes in regulation; the second describes the impact of a change in population densities on the regulating factors. These two vectors turn out to be very important in our analysis. The first one,

$$\mathbf{S}_i=\frac{\partial r_i}{\partial \mathbf{R}}, \tag{4}$$

is the *sensitivity niche vector*. Originally it was defined with an extra minus sign in Meszéna et al (2006) to imply resource depletion – but, since the generalized regulating factors could be anything, not just resources, we will not use this convention here. The other quantity,

$$\mathbf{I}_j=\frac{\partial \mathbf{R}}{\partial x_j}, \tag{5}$$

is the *impact niche vector* (the $\mathbf{C}$ of Meszéna et al 2006). Again, we use a slightly different convention: originally the impact vector was the derivative of $\mathbf{R}$ with respect to $n_j=\exp(x_j)$, not x_j. This is to make the formalism consistent with what will follow in Section 4. These vectors may be calculated for any population size, but their real utility comes through when evaluated at equilibrial densities, as they are in Eq. (3).

Let us define the community matrix as the product of the two niche vectors:

$$a_{ij} = \mathbf{S}_i \mathbf{I}_j = \frac{\partial r_i}{\partial \mathbf{R}} \frac{\partial \mathbf{R}}{\partial x_j} = \frac{\partial r_i}{\partial x_j}, \tag{6}$$

where, as before, summation or integration for all indices of $\mathbf{R}$ is assumed.

With these notations and conventions established, Eq. (3) can be rewritten as

$$\frac{\partial r_i}{\partial E} + \sum_{j=1}^{L} a_{ij} \frac{\mathrm{d}x_j^*}{\mathrm{d}E} = 0. \tag{7}$$

Rearranging and inverting the community matrix solves this system of equilibrium equations:

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L} a_{ij}^{-1} \frac{\partial r_j}{\partial E}, \tag{8}$$

or

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\frac{1}{J} \sum_{j=1}^{L} \hat{a}_{ij} \frac{\partial r_j}{\partial E}, \tag{9}$$

where J and $\hat{a}_{ij}$ are the determinant and the classical adjoint of a_{ij}, respectively. Also, it is understood that the inverse operation a_{ij}^{-1} always refers to inverting the whole matrix as opposed to calculating the inverses of the individual matrix elements.

Small values of $|J|$ indicate weak community regulation and strong dependence on population densities so that even a slight change in abundance may drive certain populations to extinction. This means that in this case coexistence is only possible for a narrow range of environmental parameters and is thus not robust. Since the determinant is simply the product of the eigenvalues, knowing all eigenvalues of a_{ij} is equivalent to knowing the determinant. More importantly, the largest eigenvalue (which will still be negative for a stable system) may be used as a proxy for the loss of robustness: as the largest eigenvalue approaches zero, so does the determinant, signaling that the system has approached a bifurcation point.

3.2 Niche

The biologically more intuitive sensitivity and impact niche vectors also have the capacity to measure robustness besides the determinant of the matrix a_{ij}. As shown in Meszéna et al (2006), it is always true that

$$|J| \leq \mathscr{V}_{\mathbf{S}} \mathscr{V}_{\mathbf{I}}, \tag{10}$$

where $\mathscr{V}_{\mathbf{S}}$ and $\mathscr{V}_{\mathbf{I}}$ refer to the volume of the parallelepipeds spanned by the sensitivity and the impact vectors of each species, respectively. Note that these volumes remain finite dimensional even if there are infinitely many regulating factors, because they are spanned by as many vectors as the number of species considered. The volume $\mathscr{V}_{\mathbf{S}}$ ($\mathscr{V}_{\mathbf{I}}$) will be zero if the collection of all sensitivity

(impact) vectors is a linearly dependent set, and will be small in the case of near linear dependence. A corollary of this is that the volumes will be small if any two vectors are nearly parallel to one another. Therefore *coexistence will not be robust if either the sensitivity or the impact vectors are too similar to each other, making* $\mathcal{V}_{\mathbf{S}}$ *or* $\mathcal{V}_{\mathbf{I}}$ *and thus the product of the two volumes small*. In theory it would be possible that a small $\mathcal{V}_{\mathbf{S}}$ is compensated by a large $\mathcal{V}_{\mathbf{I}}$ leading to robust coexistence, but in practice this probably never happens. On the contrary, a small (large) value of one of the volumes usually implies a small (large) value of the other, since corresponding sensitivity and impact vectors tend to be similar – a mathematical way of saying the biological fact that a population will generally use and therefore influence the same resources that it depends upon for its survival. In conclusion, species have to differ in their responses to the regulating factors as well as in the way they modify them if they are to coexist robustly. Similarity of species is measured by the volumes spanned by the sensitivity and impact vectors, two quantities that can mechanistically and very simply be obtained from the model definition (though usually the numerical values of the equilibrium densities also need to be known). The more orthogonal the vectors of the species, the less similar they are. Coexistence of similars is not impossible but sensitive to perturbations of the environment, as is the coexistence of species that are weakly regulated (indicated by niche vectors of small length), since in both cases the volumes defined by the vectors will be small. The general way of making this instability more robust is to make regulation stronger and the coexisting species less similar, i.e. making the vectors longer and more orthogonal to one another.

Leibold (1995), and Chase and Leibold (2003) already introduced a modernized ecological niche concept that was based on the two-way interaction between a population and its environment. Their version of the impact vector is almost identical to ours. Our sensitivity vector is the normal vector of the zero net growth isocline (ZNGI) describing Leibold's concept of the requirement niche. We consider only the slope, but not the location, of the ZNGI as a descriptor of the niche, because the impact and sensitivity niche vectors thus defined are the proper generalizations of the Hutchinsonian resource utilization function describing the partitioning of the niche space: their scalar product (overlap) yields the competition coefficients (see Pigolotti et al 2008 for the case of classical resource continua).

The essential aspect of the Hutchinsonian niche space is that coexisting species avoid competitive exclusion via partitioning that space (Hutchinson 1978). In the context of the described theory, the species should differ with respect to the regulating variables. Therefore, the proper concept of niche space is that of *the set of all regulating factors*. The impact and sensitivity niche vectors can be seen as the generalization of the resource utilization function. In the case of a continuum of regulating variables, the continuous index (like the food size q in the example in Section 2) constitutes the "niche variable" or "niche axis". To allow for generality while keeping the spirit of Hutchinson's parlance, one may want to refer to the discrete indices of the regulating variables also as (discrete) niche variables. Then, the niche space to be partitioned is the space spanned by the niche variables. It should not be confused with the space of regulating factors (or regulation space), which is the space of all the possible combination of values the regulating factors may assume. For instance, in the case of the food size continuum, niche space is one dimensional, while regulation space is the

infinite dimensional function space of the functions $R(q)$ (see Fig. 1 for a visual representation of this difference).

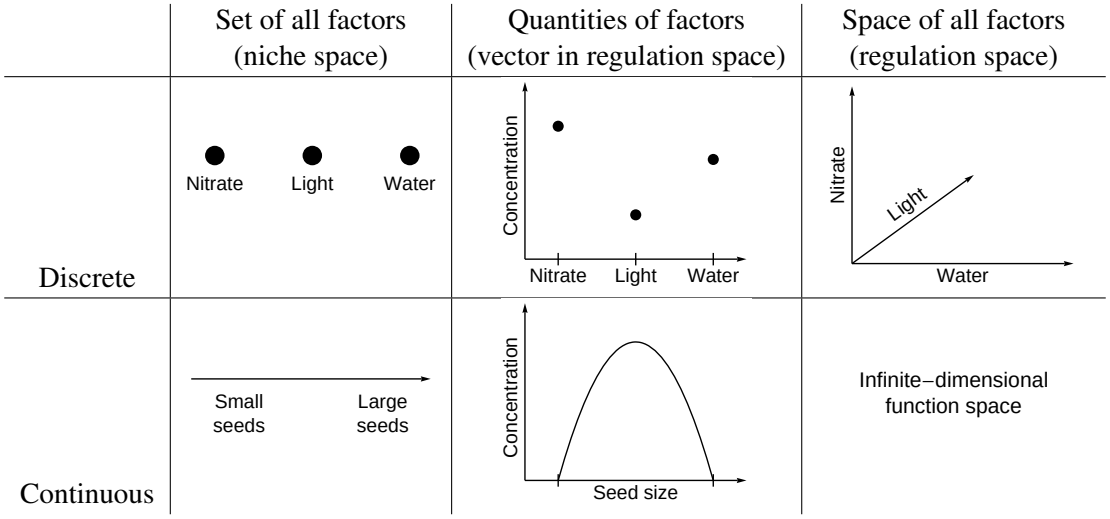

Figure 1: Niche space and regulation space for the cases of discrete (upper row) and continuous (lower row) resources. The discrete case is exemplified by three resources (regulating factors): nitrate (NO_3^-), light (photosynthetically active radiation, PAR) and water (H_2O). Now the niche space (defined as the set of regulating factors) is a 3-element set (left figure). These resources are always present in specific quantities; the central figure in the upper row plots these three numbers. They form a vector of three components, a specific realization of the vector **R**. The regulation space (figure on the right) is the vector space that contains all possible vectors **R**. Having three distinct regulating factors (i.e. a 3-element niche space) means that the regulation space is three dimensional. In the continuous case we assume the existence of a fine gradation of various seed sizes that a hypothetical bird community may consume. That is, between the limits defined by the smallest and largest possible size, all seed sizes are available and are potentially regulating. The niche space therefore has infinitely many elements: one for each seed size. These elements are linearly ordered, creating a one-dimensional space (left figure of lower row). As in the discrete case, one may plot resource availabilities for all seed sizes – but this time, instead of a vector, one obtains a function (central figure of lower row). The space that contains all these possible functions has infinitely many dimensions and thus it is impossible to visualize on paper. Notice however that while the regulation space is infinite dimensional, niche space has only one dimension and is easily visualizable.

4 Extending the theory to periodic orbits

Recall the general continuous-time dynamical equations of the system (Eq. 1):

$$\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} = r_i\left(\mathbf{R}(x_1(t),\ldots,x_L(t)),E,t\right) \qquad (i=1,\ldots,L). \tag{1}$$

Now we shall assume that the L-component vector field defined by the right hand side of Eq. (1) induces a unique, stable, periodic flow $\varphi_i(x_1^0,\ldots,x_L^0,E,t)$ with period T and initial conditions $x_i^0 = x_i(0)$, where the initial moment t_0 was chosen to be zero without loss of generality. It is a very important restriction at this point however that we assume T not to change in response to perturbations – in other words, we assume that it is independent of E. This assumption is more or less reasonable when the source of the periodicity is external forcing like seasonality, but usually breaks down if the cycles are internally generated by the dynamics.

Now, if we were able to translate the system into an equivalent *discrete* model with time step T, then this new system would possess a fixed point to which one could apply the formalism of the previous section. More specifically, let us write the logarithms of the discrete rates of growth $\bar{r}_i$ that we obtain by stroboscopically recording the state of the system defined by (1) every time T. Various expressions are possible, the more useful of which are

$$\bar{r}_i(x_1^0,\ldots,x_L^0,E) = \int_0^T r_i(\tau)\,\mathrm{d}\tau \tag{11}$$

and

$$\bar{r}_i(x_1^0,\ldots,x_L^0,E) = \Pi_i(x_1^0,\ldots,x_L^0,E) - x_i^0, \tag{12}$$

where r_i are the growth rates as defined by the right hand side of Eq. (1), τ is the time integration variable and Π_i is the so-called stroboscopic (or Poincaré) map. This map transforms the initial densities into the densities one period later, so that by definition

$$\Pi_i(x_1^0,\ldots,x_L^0,E) = \varphi_i(x_1^0,\ldots,x_L^0,E,T) = x_i(T). \tag{13}$$

When the dynamics is flowing on the periodic attractor, $\bar{r}_i(x_1^*,\ldots,x_L^*,E) = 0$, where x_i^* are the equilibrium initial conditions (to which the system returns after time T). Naturally, all the x_i^* are functions of E. Implicit differentiation of this condition with respect to E yields

$$\frac{\partial \bar{r}_i}{\partial E} + \sum_{j=1}^{L} \frac{\partial \bar{r}_i}{\partial x_j^0}\frac{\mathrm{d}x_j^*}{\mathrm{d}E} = 0. \tag{14}$$

Rearranging the equation and inverting the matrix multiplying the second term above, we get

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L}\left(\frac{\partial \bar{r}_i}{\partial x_j^0}\right)^{-1}\frac{\partial \bar{r}_j}{\partial E}. \tag{15}$$

Now the only thing left to be done is to express the derivatives of $\bar{r}_i$ in terms of the continuous dynamics. The response of $\bar{r}_i$ to changes of the external parameters is expressible from Eq. (11) as

$$\frac{\partial \bar{r}_i}{\partial E} = \int_0^T \frac{\partial r_i(\tau)}{\partial E}\,\mathrm{d}\tau. \tag{16}$$

The derivative of $\bar{r}_i$ with respect to the initial conditions may be obtained using the stroboscopic map:

$$\frac{\partial \bar{r}_i}{\partial x_j^0} = \frac{\partial \Pi_i}{\partial x_j^0} - \frac{\partial x_i^0}{\partial x_j^0}, \tag{17}$$

which is shown to be

$$\frac{\partial \bar{r}_i}{\partial x_j^0} = \mathscr{T}\mathrm{Exp}\left(\int_0^T \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)} \mathrm{d}\tau\right) - \delta_{ij} \tag{18}$$

in Appendix A. Apart from the calculation leading to the above Jacobian for the stroboscopic map, Appendix A also contains the definitions for the time-ordering operator $\mathscr{T}$ and the matrix exponential Exp therein (δ_{ij} is the identity matrix). As before, summation or integration for all indices of $\mathbf{R}$ is assumed in the exponent above.

Substituting Eqs. (16) and (18) into Eq. (15), we finally arrive at

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L} \left(\mathscr{T}\mathrm{Exp}\left(\int_0^T \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)} \mathrm{d}\tau\right) - \delta_{ij}\right)^{-1} \int_0^T \frac{\partial r_j(\tau)}{\partial E} \mathrm{d}\tau. \tag{19}$$

This formula looks considerably more complicated than its equilibrium analogue (Eq. 8), but the interpretation will turn out to be the same. Let us define the time-dependent niche vectors in the following way. The sensitivity will be

$$\mathbf{S}_i(\tau) = \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \tag{20}$$

for every moment $\tau \in [0, T)$. Similarly, the impact for any moment will be

$$\mathbf{I}_j(\tau) = \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)} = \frac{\partial \mathbf{R}(\tau)}{\partial n_j(\tau)} n_j(\tau), \tag{21}$$

where the form of the vector has also been indicated on the linear scale, since that will be more useful for applications later on.

We shall see that these vectors have the capacity to measure the robustness of the system – just as they did in the fixed point case. The scalar product of these two vectors for all indices of the regulating factors will yield a community matrix for every moment τ:

$$a_{ij}(\tau) = \mathbf{S}_i(\tau)\mathbf{I}_j(\tau) = \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)}. \tag{22}$$

Notice however that the exponent in Eq. (19) contains not just the scalar product of the sensitivity and impact vectors, but this product integrated over time. Let us denote the integral of $a_{ij}(\tau)$ with A_{ij}:

$$A_{ij} = \int_0^T a_{ij}(\tau)\,\mathrm{d}\tau = \int_0^T \frac{\partial r_i(\tau)}{\partial \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j(\tau)} \mathrm{d}\tau. \tag{23}$$

In this formula we sum or integrate over all indices of $\mathbf{R}$, plus integrate over time. The time integration is in principle no different from all the other integrals/summations involved: as a matter of formal analogy, we could even say that τ is just another continuous quantity indexing the vector of regulating factors, for which we need to integrate over the interval $[0,T)$. This observation allows us to redefine the concept of a regulating factor. Instead of considering $\mathbf{R}(\tau)$ a different vector for every moment τ, we can regard the function $\tau \mapsto \mathbf{R}(\tau)$ as a *single* vector of regulating factors with the extra continuous index τ (cf. Meszéna and Metz in press). If we accept this formal analogy between resource continua and time, then the cyclic time variable τ itself becomes a niche variable. Let us call the vector $\mathbf{R}(\tau)$ at any one particular moment τ the *instantaneous* vector of regulating factors, and $\mathbf{R}(\cdot)$, where τ plays the role of an index, the *temporal* vector of regulating factors. All quantities carrying these same indices (i.e. time-dependent boldface ones) should inherit this nomenclature, therefore we may talk about instantaneous and temporal sensitivity and impact vectors as well. For the purposes of our theory, the temporal niche vectors are the ones we need, as opposed to the instantaneous ones.

Eq. (19) can be rewritten in terms of A_{ij}:

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L} \left(\mathscr{T}\mathrm{Exp}(A_{ij}) - \delta_{ij} \right)^{-1} \int_0^T \frac{\partial r_j(\tau)}{\partial E} \, \mathrm{d}\tau. \tag{24}$$

The matrix A_{ij} is the scalar product of the *temporal* sensitivity and impact vectors for all indices of $\mathbf{R}(\cdot)$ (which therefore includes time). If any two species have very similar temporal sensitivity (impact) vectors, the determinant of A_{ij} will be small. The question is: does a small $\det A_{ij}$ imply that $\det(\mathscr{T}\mathrm{Exp}(A_{ij}) - \delta_{ij})$ will also be small and thus the response of the equilibrium densities large? This question is answered affirmatively in Appendix B, implying that *the product of the volumes spanned by the temporal sensitivity and impact vectors – cf. Inequality (10) – is the proper measure of robustness in our context*. Therefore we may conclude that the biological content of Eq. (19) is exactly equivalent to the meaning of Eq. (8). Treating every regulating factor at every moment within one period as a *different* regulating factor defines the full space of regulating variables now, and each species has a fixed *temporal* sensitivity and impact vector in this extended space. This linear space of functions is the one in which the volumes spanned by the niche vectors have to be calculated. We will refer to the corresponding extended niche space (the *set* of regulating factors) as the temporal niche space (see Fig. 2).

Naturally, the regulating factors at different times cease to be different from one another in the absence of fluctuations. This intuitively obvious fact can be demonstrated mathematically by showing that Eq. (19) simplifies to the time-independent Eq. (8) if the attractor of the dynamics is a fixed point instead of a limit cycle. In that case, the "period" T can be chosen arbitrarily, so let us choose an infinitesimal $\mathrm{d}\tau$ for the period. Then Eq. (19) will read

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L} \left(\mathscr{T}\mathrm{Exp}\left(\frac{\partial r_i}{\partial \mathbf{R}} \frac{\partial \mathbf{R}}{\partial x_j} \mathrm{d}\tau \right) - \delta_{ij} \right)^{-1} \frac{\partial r_j}{\partial E} \, \mathrm{d}\tau. \tag{25}$$

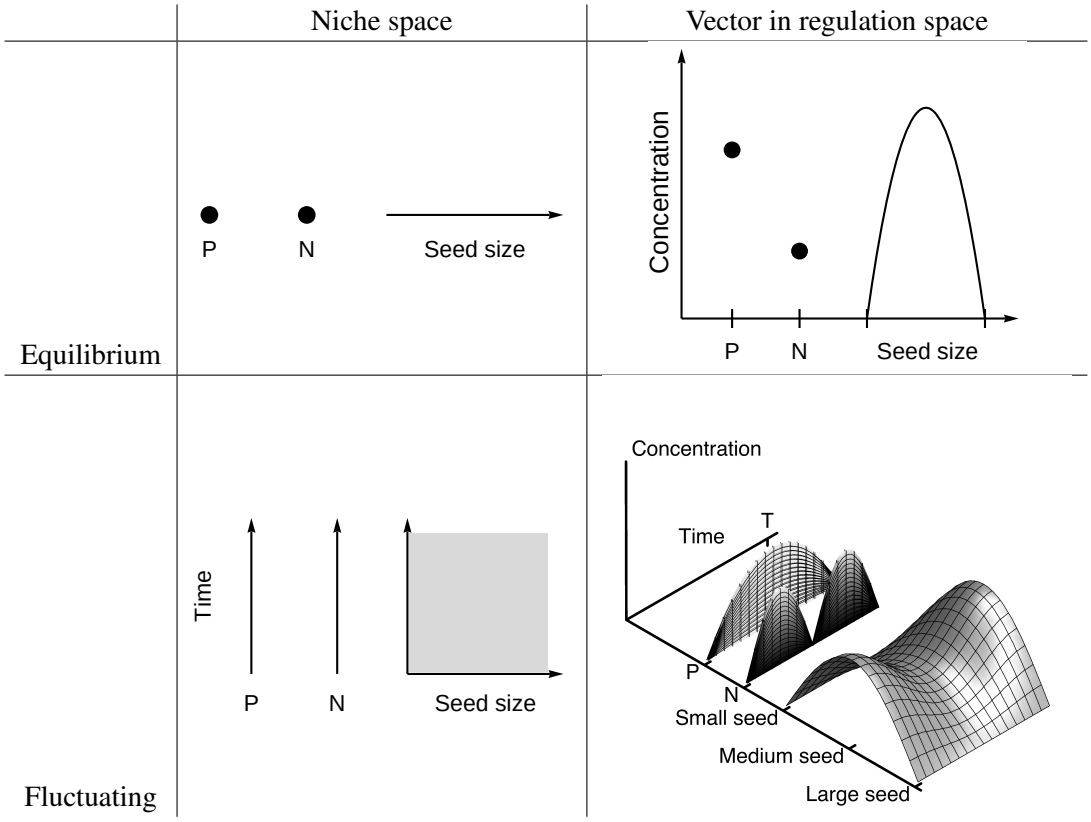

Figure 2: Instantaneous and temporal niche and regulation space for a hypothetical bird community. The birds feed on seeds of various sizes, use specific nesting sites (N), and are preyed upon by a predator (P). The first row depicts an equilibrium community: the left side shows the niche space, the right side shows a sample element of regulation space (i.e. a specific vector $\mathbf{R}$). The second row does the same, but for the temporal niche and regulation spaces, where every regulating factor at every moment is a different factor, leading to the temporal $\mathbf{R}(\cdot)$ on the right side. Notice that the dimension of the niche space has increased by one.

Since the matrix in the exponent is now a constant, time-ordering (see Appendix A) does not play a role and thus the exponential function can be Taylor expanded to linear order in time:

$$\frac{\mathrm{d}x_i^*}{\mathrm{d}E} = -\sum_{j=1}^{L}\left(\delta_{ij} + \frac{\partial r_i}{\partial \mathbf{R}}\frac{\partial \mathbf{R}}{\partial x_j}\mathrm{d}\tau - \delta_{ij}\right)^{-1}\frac{\partial r_j}{\partial E}\mathrm{d}\tau = -\sum_{j=1}^{L}\left(\frac{\partial r_i}{\partial \mathbf{R}}\frac{\partial \mathbf{R}}{\partial x_j}\right)^{-1}\frac{\partial r_j}{\partial E}, \tag{26}$$

which is identical to Eq. (8). As expected, our theory contains the equilibrium situation as a special case.

See Appendix D for an alternative derivation and form of the niche vectors that is interesting but awkward from a computational point of view.

5 Example: a minimal model of purely fluctuation-maintained coexistence

Here we apply our formalism to a minimal model of temporal niche segregation. It is a two-species Lotka–Volterra model with periodic $r_0(t)$ and $K(t)$ parameters, and competition coefficients that are all equal to one. This means that the determinant of the community matrix will be zero at any one moment: coexistence is maintained purely by fluctuations. This assumption is not necessary for fluctuations to have a stabilizing effect – however, we want to focus strictly on the effects of fluctuations and not have any other mechanisms that might contribute to coexistence; hence the choice for our competition coefficients.

Formally, the model is defined as

$$\frac{1}{n_i(t)}\frac{\mathrm{d}n_i(t)}{\mathrm{d}t} = r_{0i}(t)\left(1-\frac{n_1(t)+n_2(t)}{K_i(t)}\right) \qquad (i=1,2) \tag{27}$$

with

$$r_{0i}(t) = \rho_i(1+r_\mathrm{e}\cos(\omega t+\phi_i)) \tag{28}$$

and

$$K_i(t) = \kappa_i(1+K_\mathrm{e}\cos(\omega t+\phi_i)). \tag{29}$$

Here ρ_i and κ_i measure the time averages of the intrinsic rate of growth and the carrying capacity of the ith population, respectively; r_e and K_e are the relative amplitudes of their fluctuations with angular frequency ω (so the period is $T = 2\pi/\omega$). Note that r_{0i} and K_i oscillate in-phase for each population. The difference $\Delta\phi = \phi_2 - \phi_1$ of the phase shifts characterizes the relative timing of the two populations.

The two populations are regulated by the same, single regulating variable: the sum of the densities. The fact that there is only one regulating factor can be made transparent by reparametrizing the model (MacArthur 1972) as a two-species competition model for a single resource $R(t)$:

$$\frac{1}{n_i(t)}\frac{\mathrm{d}n_i(t)}{\mathrm{d}t} = b_i(t)R(t) - m_i(t) \qquad (i=1,2), \tag{30}$$

and

$$R(t) = R_0 - n_1(t) - n_2(t). \tag{31}$$

Here we assumed fast resource dynamics; R_0 corresponds to the maximum possible amount of resource. The factor

$$b_i(t) = \frac{r_{0i}(t)}{K_i(t)} \tag{32}$$

characterizes the resource dependence of the population and

$$m_i(t) = \left(\frac{R_0}{K_i(t)} - 1\right) r_{0i}(t) \tag{33}$$

can be seen as the resource-independent mortality rate.

For constant parameters the single regulating factor allows for the robust persistence of only one species. In this situation the model reduces to the well-known case of density-dependent selection (Metz et al 2008): competition is won by the species with the higher K_i value (K-selection, MacArthur 1962), or – equivalently – by the species with the lower equilibrium resource level (R^* rule, Tilman 1982).

The issue of interest is that oscillations of the parameters result in a periodic solution. In turn, periodicity of the solution transforms the single regulating variable R into the *continuum* of regulating factors $R(\cdot)$. With this in mind, let us calculate the temporal sensitivity and impact vectors (functions) from Eqs. (30) and (31):

$$\mathbf{S}_i = S_i(t) = \frac{\partial r_i(t)}{\partial R(t)} = b_i(t), \tag{34}$$

and

$$\mathbf{I}_j = I_j(t) = \frac{\partial R(t)}{\partial n_j(t)} n_j(t) = -n_j(t). \tag{35}$$

The sensitivities are equivalent to the birth rates at each moment, assuming the available total resource is unity (see Eq. 30). The populations are more sensitive when their per-unit-resource birth rates are high and less so when they are low. The magnitudes of the impacts are simply measured by the population densities. This in effect means that the per capita impacts are all the same: each individual consumes exactly one unit of resource in a unit time, therefore the total consumption per unit time is simply the total density. The negative sign of the impacts indicates that the populations *reduce* the amount of resource available. Should our model be formulated for two populations who compete indirectly via a shared predator (apparent competition, Holt 1977) instead of a shared resource, the impacts would be positive, since the presence of the populations will tend to increase the predator population, not reduce it.

The community matrix will be the scalar product of $S_i(t)$ and $I_j(t)$ in time:

$$A_{ij} = \int_0^T S_i(\tau) I_j(\tau)\,\mathrm{d}\tau = -\int_0^T b_i(\tau) n_j(\tau)\,\mathrm{d}\tau = -T\,\overline{b_i n_j} = -T\left(\overline{b_i}\,\overline{n_j} + \mathrm{Cov}\left(b_i, n_j\right)\right), \tag{36}$$

where we used the identity $\overline{pq} = \overline{p}\,\overline{q} + \mathrm{Cov}(p,q)$, the overline denoting time averaging and $\mathrm{Cov}(p,q)$ being the covariance of p and q. Note that a lack of covariance between b_i and n_j leads to $\det A_{ij} = \det\left(-T\,\overline{b_i}\,\overline{n_j}\right) = 0$. Therefore, nonzero covariance between the densities and the b_is is a requirement for robust coexistence. Obviously, the constant case violates this requirement. This covariance is the same one that is so essential to Chesson's (1994) general theory of the temporal storage effect.

It is instructive to calculate $b_i(t)$ for small fluctuations, i.e. for small r_e and K_e:

$$b_i(t) = \frac{\rho_i(1 + r_\mathrm{e}\cos(\omega t + \phi_i))}{\kappa_i(1 + K_\mathrm{e}\cos(\omega t + \phi_i))} \approx \frac{\rho_i}{\kappa_i}\left(1 + (r_\mathrm{e} - K_\mathrm{e})\cos(\omega t + \phi_i)\right). \tag{37}$$

Observe that $b_i(t)$ oscillates in-phase with $r_{0i}(t)$ and $K_i(t)$ for $r_\mathrm{e} > K_\mathrm{e}$, but in opposite phase for $r_\mathrm{e} < K_\mathrm{e}$. The other constituent of the covariance, n_i, would reach K_i in a constant environment. In the case of a fluctuating $K_i(t)$, one can expect $n_i(t)$ to follow the changes in $K_i(t)$ with some phase delay. Therefore, if $r_e > K_e$ and the r_{0i}s are large enough to minimize the delay of the n_is, then b_i and n_i oscillate nearly in phase. In this case, each population becomes sensitive to resource concentration levels at the time period when it uses the resource most intensively. If $\Delta\phi$ differs from zero significantly, this situation corresponds exactly to the traditional concept of niche segregation: the resources at different instants of time are considered different, and each population depends on the very same resource which it uses. Consequently, we expect robust coexistence with the described parameter combination.

These results are in line with a more Chessonesque analysis of the same model. The application of Chesson's framework to this model can be found in Appendix C. There we find that the only coexistence mechanism operating is the storage effect, which reads

$$\Delta I = \frac{\rho_i}{\kappa_i}(r_e - K_e)\big(\mathrm{Cov}(E_r n_r) - \mathrm{Cov}(E_i n_r)\big) \tag{38}$$

in our model. Compare the two covariance terms above with the expression for the community matrix A_{ij} that we obtained with Eq. (36). At first they might look different, but if one applies the small fluctuation approximation in Eq. (37) to the community matrix then $A_{11} - A_{21}$ ($r = 1$, $i = 2$) will precisely correspond to ΔI. In Chesson's approach, the difference of the elements in one column of A_{ij} gives the storage effect; in ours, robustness is determined by $\det A_{ij}$. The difference in our approaches has its roots in the fact that Chesson uses invasion criteria to assess coexistence, whilst we are interested in stability only in the vicinity of the attractor. Calculating the difference of the column elements corresponds to the first approach, since the invasibility criterion in the Lotka–Volterra model is that intraspecific competition has to be greater than interspecific competition within the resident (so $A_{11} - A_{21} > 0$ means Species 2 can invade Species 1). On the other hand, we also know that the fixed point of stable coexistence in the same model disappears precisely when the determinant of the community matrix becomes zero, so what we are doing is simply measuring how close the system is to this critical point. Therefore, the difference between the two approaches is the particular coexistence criterion they consider, which are equivalent in the context of the Lotka–Volterra model.

The simulations (not shown) confirmed that if the two populations have identical parameters except for $\Delta\phi$, their average densities are the same, and only the relative phases in which they oscillate varies. Then we gave a small relative advantage of 10^{-4} to Species 1 by increasing κ_1. In the various runs the phase difference $\Delta\phi$ was gradually decreased from π to near zero. As expected, decreasing $\Delta\phi$ increases the response of the average densities to the perturbation of κ_1 (Fig. 3 (a) and (b)). Coexistence proved to be robust when the two oscillations were out of phase ($\Delta\phi = \pi$, corresponding to the kind of parameter combination described above). Lower values of $\Delta\phi$ resulted in significant reduction of the average density of the species with the smaller κ, however (Fig. 3 (c) and (d)). Having obtained the community matrix A_{ij} by numerically integrating over one full period, its determinant was calculated as a function of $\Delta\phi$ (Fig. 4). Observe that the determinant becomes

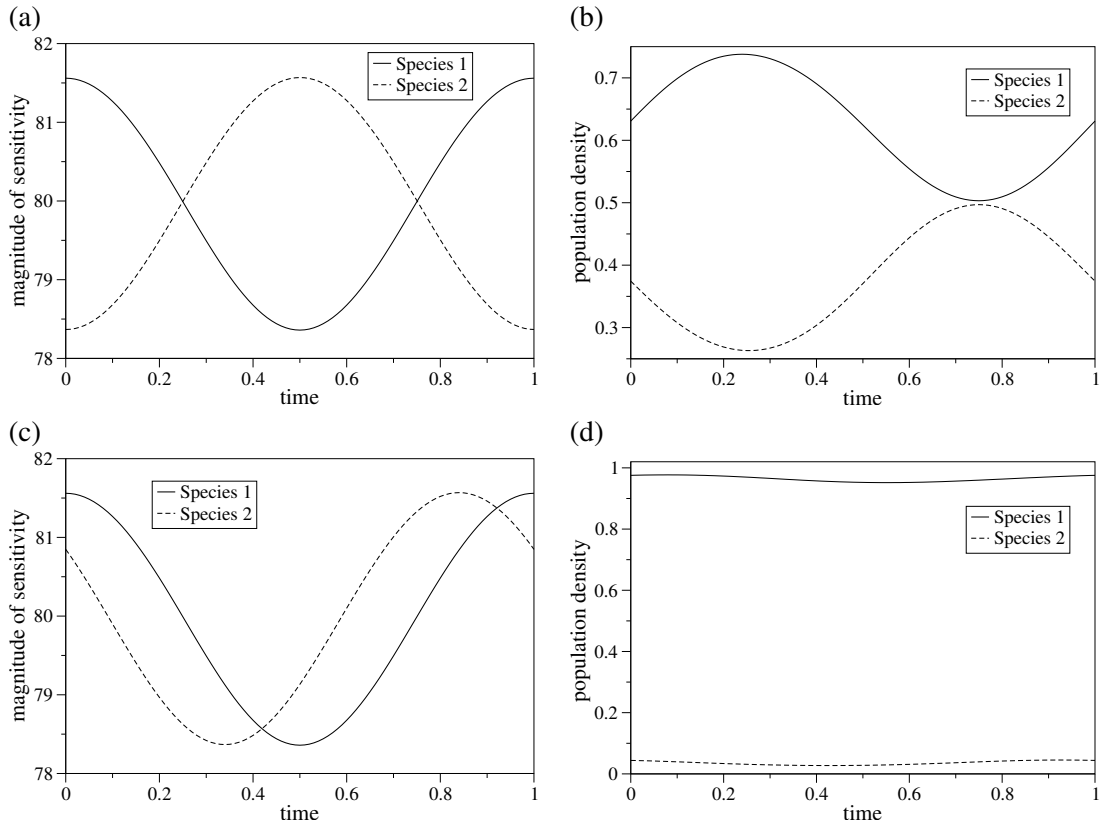

Figure 3: Top row: robust coexistence maintained by out-of-phase oscillations ($\Delta\phi = \pi$). The sensitivities $S_1(t)$ and $S_2(t)$ are shown in (a) over one full period; (b) shows the population densities $n_1(t)$ and $n_2(t)$, which are equal to the impacts $I_1(t)$ and $I_2(t)$ times (-1). Since both of these quantities oscillate out of phase, they exhibit reduced similarity, leading to robust coexistence. Bottom row: unrobust coexistence with a smaller phase difference ($\Delta\phi = 0.32\pi$). Observe on (c) that the sensitivities $S_1(t)$ and $S_2(t)$ have almost maximal similarity, and on (d) that the density $n_2(t)$ of Species 2 is very small: any further decrease of the phase difference could cause it to go extinct. Parameters: $\kappa_1 = 1.0001$, $\kappa_2 = 1$, $K_\mathrm{e} = 0.02$, $\rho_1 = \rho_2 = 80$, $r_\mathrm{e} = 0.04$, $T = 1$, $\phi_1 = 0$ (therefore $\phi_2 = \Delta\phi$).

very small around $\Delta\phi \sim 0.32\pi = 1$. This is consistent with the results in the lower row of Fig. 3, where the 10^{-4} relative disadvantage of Species 2 almost leads to its extinction at $\Delta\phi = 0.32\pi$.

6 Discussion

In this paper we extended Meszéna et al's (2006) theory of coexistence and niche from fixed point dynamics to cycles of constant period, without any constraints on the amplitude of the fluctuations.

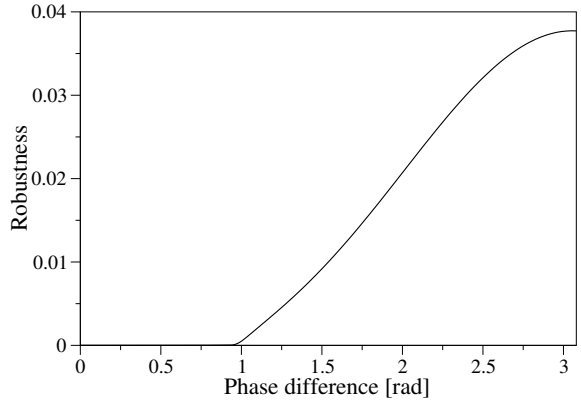

Figure 4: Loss of robustness with increasing similarity. Horizontal axis: phase difference $\Delta\phi$ in radians; vertical axis: determinant of A_{ij} as a measure of robustness. For practical purposes, $\det A_{ij}$ becomes almost zero when $\Delta\phi \lesssim 1$; it becomes exactly zero at $\Delta\phi = 0$. The curve is smooth everywhere, though it does change very rapidly around $\Delta\phi \approx 1$.

The emerging picture is a formalization of the concept of temporal niche segregation. The original theory required species to segregate with respect to the variables involved in their regulation as a condition for robust coexistence. Accordingly, temporal niche segregation means segregation with respect to the timing of population regulation within the cycle: this is done by considering the values of a given regulating variable at different instants of time within the period as different regulating variables. Generally, the niche of a species is characterized by the species' impact on and sensitivity towards the regulating variables. For the cyclic case it means that the time-courses of the impacts and the sensitivities within a period should differ between the species.

In principle, our treatment was independent of whether the cyclic dynamics originates from external forcing or from the internal dynamics of the system. However, we assumed that the period T was unaffected by the perturbations, with respect to which robustness was considered. This condition is naturally satisfied in the case of external forcing, but is usually invalid otherwise, i.e. when the cycles are generated internally by the dynamics.

Our study was motivated by the wish to have a unified mathematical theory of the ecological niche. After the Lotka–Volterra model had fallen out of favor because of its uneasy relationship with empirical details, it became the prevailing attitude to study coexistence in specific mechanistic models and have generalized conclusions only on a verbal level. As the assumptions and conclusions of the different models are often difficult to compare, and no model is immune to the criticism of neglegting important details, the predictive power of this approach is limited. Instead we prefer to have a consistent theory with clear mathematical foundations on the general level that maintains a well-defined connection to verbal theory as well as to specific models of arbitrary detailedness. Adaptive dynamics (Geritz et al 1998, Meszéna et al 2005) and the theory of structured populations (Caswell 2001, Diekmann et al 2003) demostrated the possibility and usefulness of

such a framework within the context of population biology. Within such a framework, there is a clean way of incorporating additional details whenever it is necessary.

The perturbation approach makes a general theory of coexistence possible. It was demonstrated that robustness of coexistence against the change of external parameters is tied to niche segregation in a well-defined sense (Meszéna et al 2006). As it is sufficient to consider small perturbations only, no generality is lost by carefully made linearization. This linearization establishes a general connection between an arbitrarily complicated model of coexistence and the Lotka–Volterra model. Unfortunately, the concept of a resource utilization function as a descriptor of the niche of a species does not generalize: one has to linearize the two legs of population regulation separately, leading to the concept of impact and sensitivity niches.

Intuitively, three types of niche segregation can (and have) been distinguished: functional, habitat, and temporal segregation (Christiansen and Fenchel 1977). Functional segregation is covered by the basic fixed point theory. Habitat segregation requires the handling of the spatial structure of populations – this has been achieved by Szilágyi and Meszéna (2009a,b), not just for spatial but for arbitrary population structure as well. Finally, temporal niche segregation in a periodic environment is what this paper was about. Parvinen and Meszéna (2009) studied a different kind of temporal segregation, one that is inherently tied to spatial structure as well: the coexistence of successional species. Szilágyi and Meszéna (2010) applied the framework to fluctuation-mediated coexistence by the effect of relative nonlinearity.

Today the reference point for any theory of coexistence in a fluctuating environment is the framework of Chesson (1994), both because of its completeness and its generality. Chesson distinguishes between two types of coexistence-affecting mechanisms that are specifically induced by environmental fluctuations (Chesson 2000): the storage effect and the effect of relative nonlinearity. The storage effect is essentially a result of temporal niche segregation, whilst the effect of relative nonlinearity emerges from a difference between the species' (nonlinear) competitive effect curves as a function of their densities. One very important question is how these mechanisms (and Chesson's whole framework) relate to ours. For one thing, the two approaches differ in their coexistence criteria: Chesson considers mutual invasibility; we only require that the population dynamical attractor be locally stable (note that mutual invasibility is a sufficient but not a necessary condition for coexistence, at least when demographic stochasticity can be ignored; see Szilágyi and Meszéna 2010). A second difference is that, strictly speaking, Chesson's theory is only valid for small fluctuations. In our framework, however, there is no limit on the amplitude of population oscillations. Regardless of the small-fluctuation approximation though, a more formal analogy can be drawn between the two approaches. If the growth rates are linear functions of the population densities, neglecting higher-order terms will not affect this property. Therefore, the resulting model in Chesson's scheme will be equivalent to a Lotka–Volterra model with fluctuating parameters. In fact, it will be the very same model as the one we used in our example (Eq. 27), provided that the amplitudes of the fluctuating parameters are not very large – i.e. after linearization according to Eq. (37). The analysis of this model using Chesson's framework is performed in Appendix C, where the results from the two approaches can be compared. This comparison formally establishes the fact

that Chesson's storage effect can be seen as temporal niche segregation, something that has often been stressed by Chesson himself (Chesson 1991, 1994, 2000).

When the growth rates are nonlinear functions of the densities, the analysis is more complicated, since relative nonlinearity might also contribute to species coexistence. Unfortunately, we cannot as yet provide a detailed formal analogy between the two frameworks in this case. We would like to emphasize, however, that our methodology does apply to models with relative nonlinearity, as long as the period of the oscillations remains fixed. This basically precludes the analysis of indigenously generated cycles, since their period will in general depend on the perturbed parameters. But other models, where periodicity is externally forced, may be analized in our way. One example is provided by the model of Szilágyi and Meszéna (2010), who considered the simplest possible model that produces relative nonlinearity. Their choice for the environmental fluctuations was a Gaussian white noise, but no essential part of the model is altered if one replaces the white noise with some periodic function. In this case, both their conclusions and ours hold simultaneously. We are thus provided with a specific model which may be studied using our method, and in which only relative nonlinearity is operating as a coexistence-affecting mechanism, to use Chesson's terminology.

We close our discussion by commenting on the status of niche theory in a nonequilibrium environment. Our framework assumes periodic dynamics. Nevertheless, we conjecture that the underlying idea, the concept of temporal niche segregation, generalizes for all stationarily fluctuating environments and ergodic situations as well, be it aperiodic stationary fluctuations or seasonally forced chaotic dynamics. The crucial point is to have an "equilibrium" condition, which then can be subjected to perturbation analysis. In the periodic case this happened to be the periodicity condition $\bar{r}_i = 0$. For arbitrary stationarily fluctuating environments it is the condition that the long-term average growth rate should be zero (Turelli 1978, Chesson 1994, Szilágyi and Meszéna 2010; see Hofbauer and Schreiber 2010, Schreiber et al 2010 for the formal proof). On the other hand, existence of a long-term environmental trend (i.e. departure from stationarity, as in the case of global climate change) invalidates our approach in an essential way. Then, our formulation applies only as an approximation. It could be a very good approximation, however. If a population survives for a sufficiently long time T, then the average growth rate $\ln(n(T)/n(0))/T$ for that time period is close to zero even if the initial and final densities $n(0)$ and $n(T)$ differ considerably. Therefore, the existence of long-term environmental trends does not essentially invalidate niche theory. It remains a null model: the real process can be seen as a perturbation of the presented theory.

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Appendix A: The Jacobian of the stroboscopic map

We want to obtain an expression for the derivative of the stroboscopic map Π_i with respect to the initial conditions x_j^0. According to the definition of Eq. (13),

$$\frac{\partial \Pi_i}{\partial x_j^0} = \left.\frac{\partial \varphi_i}{\partial x_j^0}\right|_{t=T} \tag{39}$$

with $x_i(t) = \varphi_i(x_1^0, \ldots, x_L^0, E, t)$ being the flow induced by the right hand side of Eq. (1) with initial conditions x_i^0. Now, let us calculate

$$\frac{\partial^2 \varphi_i}{\partial t\, \partial x_j^0} = \frac{\partial}{\partial x_j^0}\left(\frac{\partial \varphi_i}{\partial t}\right) = \frac{\partial}{\partial x_j^0} r_i(\mathbf{R}(x_1(t), \ldots, x_L(t)), E, t) = \sum_{k=1}^{L} \frac{\partial r_i(t)}{\partial \mathbf{R}(t)} \frac{\partial \mathbf{R}(t)}{\partial x_k(t)} \frac{\partial \varphi_k}{\partial x_j^0}, \tag{40}$$

where summation or integration for all indices of $\mathbf{R}$ is understood. The equation we have ended up with reads

$$\frac{\partial}{\partial t}\left(\frac{\partial \varphi_i}{\partial x_j^0}\right) = \sum_{k=1}^{L} \frac{\partial r_i(t)}{\partial \mathbf{R}(t)} \frac{\partial \mathbf{R}(t)}{\partial x_k(t)} \frac{\partial \varphi_k}{\partial x_j^0}, \tag{41}$$

where the derivative of r_i with respect to $\mathbf{R}$ and of $\mathbf{R}$ with respect to $x_k(t)$ are evaluated at the flow on the attractor. Since $\varphi_i(0) = x_i^0$ by definition, the initial condition to this equation is

$$\left.\frac{\partial \varphi_i}{\partial x_j^0}\right|_{t=0} = \delta_{ij}. \tag{42}$$

Let us introduce some simplifying notation, with $\Phi(t)$ being the derivative of the flow with respect to the initial conditions, and $a(t)$ being the time-dependent coefficient matrix multiplying $\Phi(t)$ on the right hand side of Eq. (41):

$$\Phi(t) = \frac{\partial \varphi_i}{\partial x_j^0} \tag{43}$$

and

$$a(t) = \frac{\partial r_i(t)}{\partial \mathbf{R}(t)} \frac{\partial \mathbf{R}(t)}{\partial x_k(t)}. \tag{44}$$

Eq. (41) can then be rewritten as

$$\frac{\mathrm{d}\Phi(t)}{\mathrm{d}t} = a(t) \cdot \Phi(t), \tag{45}$$

with the initial condition translating to $\Phi(0) = 1$.

The solution to the matrix differential equation (45) is nontrivial as the matrices $a(t_1)$ and $a(t_2)$ do not necessarily commute for $t_1 \neq t_2$. To handle the problem, we first define the matrix $\mathrm{Exp}(a)$, the exponential of the matrix a, by substituting a into the usual Taylor series of the exponential function. Note that $\mathrm{Exp}(a(t_1) + a(t_2)) \neq \mathrm{Exp}(a(t_1)) \cdot \mathrm{Exp}(a(t_2))$ except when the matrices $a(t_1)$

and $a(t_2)$ commute. The solution of Eq. (45) can now be written as an infinite product of matrix exponentials:

$$\begin{aligned}\Phi(t) &= \lim_{\Delta t\to 0} \mathrm{Exp}(a(t-\Delta t)\Delta t)\cdot\ldots\cdot\mathrm{Exp}(a(\Delta t)\Delta t)\cdot\mathrm{Exp}(a(0)\Delta t)\\ &= \lim_{\Delta t\to 0}\prod_{\tau=N-1}^{0}\mathrm{Exp}\left(a(\tau\Delta t)\Delta t\right),\end{aligned} \tag{46}$$

where $N = t/\Delta t \to \infty$. It is easy to show that this is indeed the solution: for an infinitesimally small Δt, Eq. (45) can be written as

$$\Phi(t+\Delta t) = \Phi(t) + a(t)\Phi(t)\Delta t = (1+a(t)\Delta t)\Phi(t) \approx \mathrm{Exp}(a(t)\Delta t)\Phi(t), \tag{47}$$

and applying this formula recursively from $t = 0$ to the final moment yields Eq. (46).

Note that the matrices within the product in Eq. (46) are ordered according to decreasing time. The expression can be made notationally more convenient by introducing the so-called time-ordering operator $\mathscr{T}$. By definition this operator rearranges a product of matrices to decreasing order in time:

$$\mathscr{T}a(t_1)\cdot a(t_2) = \mathscr{T}a(t_2)\cdot a(t_1) = \begin{cases} a(t_1)\cdot a(t_2) & \text{if } t_2 \le t_1,\\ a(t_2)\cdot a(t_1) & \text{if } t_2 > t_1.\end{cases} \tag{48}$$

This somewhat obscure but very useful notation, widely used in quantum field theory (see e.g. Weinberg 1995, p. 143), allows us to write Eq. (46) in the simple form

$$\Phi(t) = \mathscr{T}\mathrm{Exp}\left(\int_0^t a(\tau)\,\mathrm{d}\tau\right). \tag{49}$$

Substituting the definitions of $\Phi(t)$ and $a(t)$ from Eqs. (43) and (44), this solution actually reads

$$\frac{\partial\varphi_i}{\partial x_j^0} = \mathscr{T}\mathrm{Exp}\left(\int_0^t \frac{\partial r_i(\tau)}{\partial\mathbf{R}(\tau)}\frac{\partial\mathbf{R}(\tau)}{\partial x_j(\tau)}\,\mathrm{d}\tau\right), \tag{50}$$

and, using Eq. (39), the final expression for the Jacobian of the stroboscopic map is

$$\frac{\partial\Pi_i}{\partial x_j^0} = \mathscr{T}\mathrm{Exp}\left(\int_0^T \frac{\partial r_i(\tau)}{\partial\mathbf{R}(\tau)}\frac{\partial\mathbf{R}(\tau)}{\partial x_j(\tau)}\,\mathrm{d}\tau\right). \tag{51}$$

Though the result looks elegant, remember that the time-ordering operator is simply a convenient mnemotechnical symbol: its real content is expressed by the infinite matrix product in Eq. (46).

Appendix B: The criterion for robustness

Suppressing indices for better readability, Eq. (19) will read

$$\frac{\mathrm{d}x^*}{\mathrm{d}E} = -\left(\mathscr{T}\mathrm{Exp}(A) - \delta\right)^{-1}\frac{\partial\bar{r}}{\partial E}, \tag{52}$$

where x^* and $\bar{r}$ stand for the vectors x_i^* and $\bar{r}_j$, respectively, $A = \int_0^T a(\tau)\,\mathrm{d}\tau$ with $a(t) = \mathbf{S}_i(t)\,\mathbf{I}_j(t)$ as introduced in Section 4, and δ is the identity matrix.

Since the inverse of a matrix is proportional to the inverse of its determinant, and the determinant will be near zero if any of the eigenvalues approach zero, the left hand side of the equation (the response of the equilibrium densities) will become large, leading to the destabilization of the equilibrium point, if any one eigenvalue of $\mathscr{T}\mathrm{Exp}(A) - \delta$ approaches zero. Our intuition is that two species having similar temporal niche vectors will lead to one of the eigenvalues being almost zero, i.e. species that are too similar cannot coexist robustly.

First we prove that linear dependence of the temporal impact (sensitivity) niches makes the matrix $\mathscr{T}\mathrm{Exp}(A) - \delta$ degenarate, i.e. having an eigenvalue of 0. Linear dependence of the temporal impact vectors means that there exists a time-independent L-dimensional vector $\alpha = (\alpha_1, \alpha_2, \ldots, \alpha_L)$ such that $\sum_{j=1}^{L} \alpha_j \mathbf{I}_j(\tau) = 0$ for all $\tau \in [0, T)$. Then, for all τ, α is a right eigenvector of the matrix $a_{ij}(\tau) = \mathbf{S}_i(\tau)\mathbf{I}_j(\tau)$ with a corresponding eigenvalue of 0. Or, using Eq. (46), α is a right eigenvector of $\mathscr{T}\mathrm{Exp}(A)$ with an eigenvaue of 1. This means that $\mathscr{T}\mathrm{Exp}(A) - \delta$ has an eigenvalue of $1 - 1 = 0$, implying our proposition. The same argument applies for the sensitivities and the left eigenvectors. Then, since eigenvalues and eigenvectors depend on the matrix elements continuously, similarity (i.e. near linear dependence) of the temporal impact or sensitivity niches leads to having an eigenvalue that is nearly zero, leading to non-robust coexistence.

Next, we will show that the product of the volumes spanned by the temporal niche vectors ($\mathscr{V}_{\mathbf{S}}\mathscr{V}_{\mathbf{I}}$) is still the proper measure of robustness: the system gradually loses its stability as this number gets closer to zero. First we verify by direct calculation that the determinant of $\mathscr{T}\mathrm{Exp}(A)$ is insensitive to time-ordering. Using Eq. (46),

$$\begin{aligned}
\det \mathscr{T}\mathrm{Exp}(A) &= \det \mathscr{T}\mathrm{Exp}\left(\int_0^T a(\tau)\,\mathrm{d}\tau\right) \\
&= \det \lim_{\Delta t \to 0} \mathrm{Exp}(a(T-\Delta t)\Delta t) \cdot \ldots \cdot \mathrm{Exp}(a(\Delta t)\Delta t) \cdot \mathrm{Exp}(a(0)\Delta t) \\
&= \lim_{\Delta t \to 0} \mathrm{Exp}(\mathrm{Tr}\, a(T-\Delta t)\Delta t) \cdot \ldots \cdot \mathrm{Exp}(\mathrm{Tr}\, a(\Delta t)\Delta t) \cdot \mathrm{Exp}(\mathrm{Tr}\, a(0)\Delta t) \\
&= \mathrm{Exp}\left(\int_0^T \mathrm{Tr}\, a(\tau)\,\mathrm{d}\tau\right) = \mathrm{Exp}\left(\mathrm{Tr} \int_0^T a(\tau)\,\mathrm{d}\tau\right) = \det \mathrm{Exp}\left(\int_0^T a(\tau)\,\mathrm{d}\tau\right) \\
&= \det \mathrm{Exp}\,(A)\,,
\end{aligned} \tag{53}$$

where $\mathrm{Tr}\, a$ denotes the trace of the matrix a.

Note that these results imply that the determinant of $\mathscr{T}\mathrm{Exp}(A) - \delta$ will become zero precisely when $\det A$ does so. Indeed, what we have is just a trivial rescaling of A, an artefact of the conversion between discrete and continuous dynamics (in Eq. (19) the equilibrium densities x_i^* are quantities of the discrete dynamics, whilst everything else is derived from the continuous equations). So we may disregard this trivial rescaling and simply use $\det A$ as the measure of robustness. Furthermore, the inequality of Eq. (10) can be applied to the matrix A to yield $|\det A| \leq \mathscr{V}_{\mathbf{S}}\mathscr{V}_{\mathbf{I}}$, demonstrating that community robustness can be measured exactly like in the equilibium case, provided that we think of the full set of regulating factors as containing every regulating factor at every moment

within the cycle as a separate factor. This also means that all the hassle of matrix exponentials and time-ordered products may be completely ignored when applying the formalism to specific models: all that matter are the temporal sensitivity and impact vectors and the volumes they span.

Appendix C: Model analysis using Chesson's (1994) framework

In this subsection we perform the analysis of the model defined by Eq. (27) in Section 5 using Chesson's formalism. For this model, Chesson's environmental and competition parameters can be chosen as

$$E_j = \cos(\omega t + \phi_j) \tag{54}$$

and

$$C_j = n_1 + n_2, \tag{55}$$

respectively. Note that $\overline{E}_j = 0$ and that the competition parameter C_j is the same for the two species. Chesson's theory applies for small fluctuations; this assumption can be implemented by choosing the parameters r_e and K_e small.

With this parametrization, the instantaneous growth rate $r_j = g_j\left(E_j(t), C_j(t)\right)$ of the model is

$$\begin{aligned} g_j\left(E_j(t), C_j(t)\right) &= \rho_j(1 + r_\mathrm{e}E_j)\left(1 - \frac{C_j}{\kappa_j\left(1 + K_\mathrm{e}E_j\right)}\right) \\ &\approx \rho_j\left(1 + r_\mathrm{e}E_j\right) - \frac{\rho_j}{\kappa_j}\left(1 + (r_\mathrm{e} - K_\mathrm{e})E_j\right)C_j \\ &= \rho_j\left(1 - \frac{C_j}{\kappa_j}\right) + \rho_j r_\mathrm{e}E_j - \frac{\rho_j}{\kappa_j}(r_\mathrm{e} - K_\mathrm{e})E_jC_j, \end{aligned} \tag{56}$$

where $\approx$ means the small fluctuation approximation. The natural reference points are $E_j^* = 0$ and $C_j^* = \kappa_j$, for which $g_j(E_j^*, C_j^*) = 0$ is satisfied, as required. Then the standardized parameters of Chesson are

$$\mathscr{E}_j = g_j(E_j, C_j^*) = \rho_j K_\mathrm{e} E_j \tag{57}$$

and

$$\mathscr{C}_j = -g_j(E_j^*, C_j) = -\rho_j\left(1 - \frac{C_j}{\kappa_j}\right). \tag{58}$$

Using these notations, the growth rate is

$$r_j \approx \mathscr{E}_j - \mathscr{C}_j + \gamma_j\mathscr{E}_j\mathscr{C}_j, \tag{59}$$

where

$$\gamma_j = -\frac{r_\mathrm{e} - K_\mathrm{e}}{K_\mathrm{e}\rho_j} \tag{60}$$

is the measure of nonadditivity. Note that since r_e was greater than K_e in our simulations, the γ_j are negative, i.e. we have a subadditive situation.

Since the competition parameter C is a linear function of the competitive factors (the two densities in this case), this model does not produce relative nonlinearity. However, there is storage effect. Chesson's formula for the storage effect reads

$$\Delta I = \gamma_i \overline{\mathscr{E}_i \mathscr{C}_i^{-i}} - \sum_r q_{ir} \gamma_r \overline{\mathscr{E}_r \mathscr{C}_r^{-i}}, \tag{61}$$

where the overline denotes time-averaging, i is the invader index, r is the resident, the $-i$ superscript means that the given quantity is to be evaluated with species i at zero density and all other species at their equilibria, and

$$q_{ir} = \frac{\partial \mathscr{C}_i^{-i}}{\partial \mathscr{C}_r^{-i}} \tag{62}$$

are factors introduced into the theory so that all linear terms in the final expression for the coexistence-affecting mechanisms cancel (this does not play a great role in our case, but becomes crucial if the competitive factors are nonlinear functions of the densities, i.e. if relative nonlinearity is operating). Let us calculate ΔI in our model. The standardized competition parameter, as given by Eq. (58), is

$$\mathscr{C}_j = \frac{\rho_j}{\kappa_j}(n_r + n_i) - \rho_j \tag{63}$$

(j is a general species index which may refer to the resident or the invader), and so

$$\mathscr{C}_j^{-i} = \frac{\rho_j}{\kappa_j} n_r - \rho_j. \tag{64}$$

The differential of this expression is

$$\mathrm{d}\mathscr{C}_j^{-i} = \mathrm{d}\left(\frac{\rho_j}{\kappa_j} n_r - \rho_j\right) = \frac{\rho_j}{\kappa_j} \mathrm{d}n_r, \tag{65}$$

therefore

$$q_{ir} = \frac{\partial \mathscr{C}_i^{-i}}{\partial \mathscr{C}_r^{-i}} = \frac{\rho_i \kappa_r}{\rho_r \kappa_i}. \tag{66}$$

Let us work a little more on the expression $\overline{\mathscr{E}_j \mathscr{C}_k^{-i}}$, using the fact that $\mathscr{E}_j = \rho_j K_e E_j$:

$$\overline{\mathscr{E}_j \mathscr{C}_k^{-i}} = \overline{\rho_j K_e E_j \frac{\rho_k}{\kappa_k}(n_r - \kappa_k)} = \frac{\rho_j \rho_k K_e}{\kappa_k} \overline{E_j n_r} \tag{67}$$

(the second term is zero, since $\overline{E}_j = 0$). Substituting all of this into Eq. (61) we get

$$\begin{aligned}
\Delta I &= \gamma_i \overline{\mathscr{E}_i \mathscr{C}_i^{-i}} - q_{ir} \gamma_r \overline{\mathscr{E}_r \mathscr{C}_r^{-i}} = \frac{K_e - r_e}{K_e \rho_i} \frac{\rho_i^2 K_e}{\kappa_i} \overline{E_i n_r} - \frac{\rho_i \kappa_r}{\rho_r \kappa_i} \frac{K_e - r_e}{K_e \rho_r} \frac{\rho_r^2 K_e}{\kappa_r} \overline{E_r n_r} \\
&= \rho_i \frac{K_e - r_e}{\kappa_i} \overline{E_i n_r} - \rho_i \frac{K_e - r_e}{\kappa_i} \overline{E_r n_r} = \rho_i \frac{K_e - r_e}{\kappa_i} \left(\overline{E_i n_r} - \overline{E_r n_r}\right) \\
&= \frac{\rho_i}{\kappa_i}(r_e - K_e)\big(\mathrm{Cov}(E_r n_r) - \mathrm{Cov}(E_i n_r)\big),
\end{aligned} \tag{68}$$

where we used Eq. (60) to evaluate γ_r. As mentioned before, $r_e - K_e$ is positive, and so is $\mathrm{Cov}(E_r n_r) - \mathrm{Cov}(E_i n_r)$, because the resident obviously correlates more strongly with its own E than with the E of the other species. It follows that $\Delta I > 0$ and so we have the storage effect.

Appendix D: An alternative form of the niche vectors

A continuous periodic system can be converted into a discrete one with a fixed point, as is done by Eq. (15), to which the whole body of theory discussed in Section 3 directly applies. The most straightforward way of extending our theory to fluctuating situations would have been to derive the sensitivity and impact vectors in the same manner as was done in Section 3, taking into account that the growth rates are actually the cumulative growths of each population during the time interval $[0,T)$ – which are all zero, as they should be. Though it is somewhat quicker to obtain the results this way, their interpretation is more difficult; hence the longer route we have taken. Nevertheless, it will be instructive to see the forms of the sensitivity and impact vectors obtained by applying the equilibrium theory to the cumulative growth rates. In other words, we want to construct the "P-level" (Point equilibrium-level) niche vectors, the ones we obtain without "looking into" the within-period dynamics, and see what their relationship is to the C-level (Cycle-level) niche vectors (the ones we have already derived).

To establish the P-level niche vectors, we first need to consider the cumulative growth of each population over one period:

$$\bar{r}_i[\mathbf{R}] = \int_0^T r_i(\mathbf{R}(x_1(t),\ldots,x_L(t)),E,t)\,\mathrm{d}\tau, \tag{69}$$

which is thus a functional of the vector of regulating factors. Now, looking at Eq. (15) shows that the evaluation of $\partial\bar{r}_i/\partial x_j^0$ will yield the P-level niche vectors. Applying the chain rule, the sensitivity will be defined by the functional derivative

$$\mathbf{S}_i^{\mathrm{P}}(\tau) = \frac{\delta\bar{r}_i}{\delta\mathbf{R}(\tau)} = \frac{\partial r_i(\tau)}{\partial\mathbf{R}(\tau)} = \mathbf{S}_i(\tau), \tag{70}$$

that is, the P-level sensitivity is exactly the same as the C-level one. The P-level impact is somewhat more involved:

$$\begin{aligned}\mathbf{I}_j^{\mathrm{P}}(\tau) &= \frac{\partial\mathbf{R}(\tau)}{\partial x_j^0} = \sum_{k=1}^{L}\frac{\partial\mathbf{R}(\tau)}{\partial x_k(\tau)}\frac{\partial\varphi_k(\tau)}{\partial x_j^0} = \sum_{k=1}^{L}\mathbf{I}_k(\tau)\mathscr{T}\mathrm{Exp}\left(\int_0^\tau\frac{\partial r_k(\tau')}{\partial\mathbf{R}(\tau')}\frac{\partial\mathbf{R}(\tau')}{\partial x_j(\tau')}\,\mathrm{d}\tau'\right)\\ &= \sum_{k=1}^{L}\mathbf{I}_k(\tau)\mathscr{T}\mathrm{Exp}\left(\int_0^\tau\mathbf{S}_k(\tau')\mathbf{I}_j(\tau')\,\mathrm{d}\tau'\right),\end{aligned} \tag{71}$$

where the time-ordered exponential expression for the derivative of the flow is derived in Appendix A. Observe that the P-level impacts are different from but still composed of the C-level niche vectors.

With the P-level niche vectors, the matrix A_{ij} becomes expressible as

$$\begin{aligned} A_{ij} = \frac{\partial \bar{r}_i}{\partial x_j^0} &= \int_0^T \mathbf{S}^{\mathrm{P}}(\tau)\mathbf{I}^{\mathrm{P}}(\tau)\,\mathrm{d}\tau = \int_0^T \frac{\delta \bar{r}_i}{\delta \mathbf{R}(\tau)} \frac{\partial \mathbf{R}(\tau)}{\partial x_j^0}\,\mathrm{d}\tau \\ &= \sum_{k=1}^{L} \int_0^T \mathbf{S}_i(\tau)\mathbf{I}_k(\tau)\mathscr{T}\mathrm{Exp}\left(\int_0^\tau \mathbf{S}_k(\tau')\mathbf{I}_j(\tau')\,\mathrm{d}\tau'\right)\mathrm{d}\tau, \end{aligned} \tag{72}$$

the scalar product of the P-level sensitivities and impacts for all regulating factors and time. This way we have established the relationship between the P-level and the more convenient C-level description.

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